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Dynamic connectivity patterns from an insular marine protected area in the Gulf of California



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ABSTRACT

We studied connectivity patterns from a small and isolated island in the Gulf of California (San Pedro Mártir Island Biosphere Reserve), as a source of propagules to surrounding Marine Protected Areas and fishing sites. We used a particle-tracking scheme based on the outputs of a three-dimensional numerical hydrodynamic model to assess the spatial domain to which the island exports larvae as well as larvae retention. We modeled the release of passive particles from locations around the island during the four release dates (May 15 and 31, and June 14 and 30), matching the lunar phases and the peak of the reproductive season for several commercial invertebrates and fish, at the time when currents in the Gulf typically reverse. For each simulation we analyzed the data at 15, 20 and 30 days after the release to represent different planktonic propagule durations. Particle dispersion was highly dynamic and spread over ~600 km along the coast over the study period. Overall, we observed potential ecological connectivity with a few key distant fishing sites that changed through time, and potential genetic connectivity towards many near and distant sites, including all neighboring Marine Protected Areas, although not simultaneously. The percentages of particles remaining within the boundaries of the island tended to decline from May to June, and decreased with delayed planktonic propagule duration. The design of effective Marine Protected Areas should acknowledge the dynamic nature of connectivity patterns, for instance, by establishing adaptive network reserves to respond to changing ocean features that match reproductive patterns of target species and fisheries behavior.

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1. Introduction

The Gulf of California (GC) is a semi-enclosed sea situated in Northwest Mexico with three marine faunal regions, the northern, central and southern (Brusca et al., 2005; Walker, 1960) (Fig. 1). Driven by low frequency currents and tides from the Pacific Ocean, and local winds, the circulation of the GC is seasonally-reversing; cyclonic in summer and anticyclonic in winter (Alvarez Borrego, 2010; Lavín and Marinone, 2003). The cyclonic phase lasts from June to September (Carrillo and Palacios-Hernández, 2002; Marinone, 2008; Palacios-Hernández et al., 2002) and includes a poleward coastal current over the mainland continental shelf in the southern

Gulf. This coastal current starts in June and quickly intensifies. Part of this current continues northward across the constriction between the large islands to form the cyclonic eddy of the northern Gulf, and part turns cyclonically to return on the peninsula side of the Gulf. The anticyclonic phase lasts from November to April, and entails the reversal of the northern Gulf eddy and the coastal current in the southern Gulf (Marinone, 2008). In addition to the seasonal circulation, there are meso-scale eddies in the southern Gulf, which have been modeled by Zamudio et al. (2008) and described in detail by Lavín et al. (2013).

The northern GC has two different oceanographic subregions, the Upper Gulf of California and the Midriff Island Region (MIR, Fig. 1), characterized each by different marine landscapes (depth, currents, bottom types) (Brusca et al., 2005). One distinctive oceanographic feature is the presence of a tidal-mixing front in the southern end of the MIR (Argote et al., 1995) which affects the distribution and exchange of sea-water between the southern and the northern Gulf (Danell-Jiménez et al., 2009; Sánchez-Velasco et al., 2009). The MIR and the front are believed to play an important role molding dispersal

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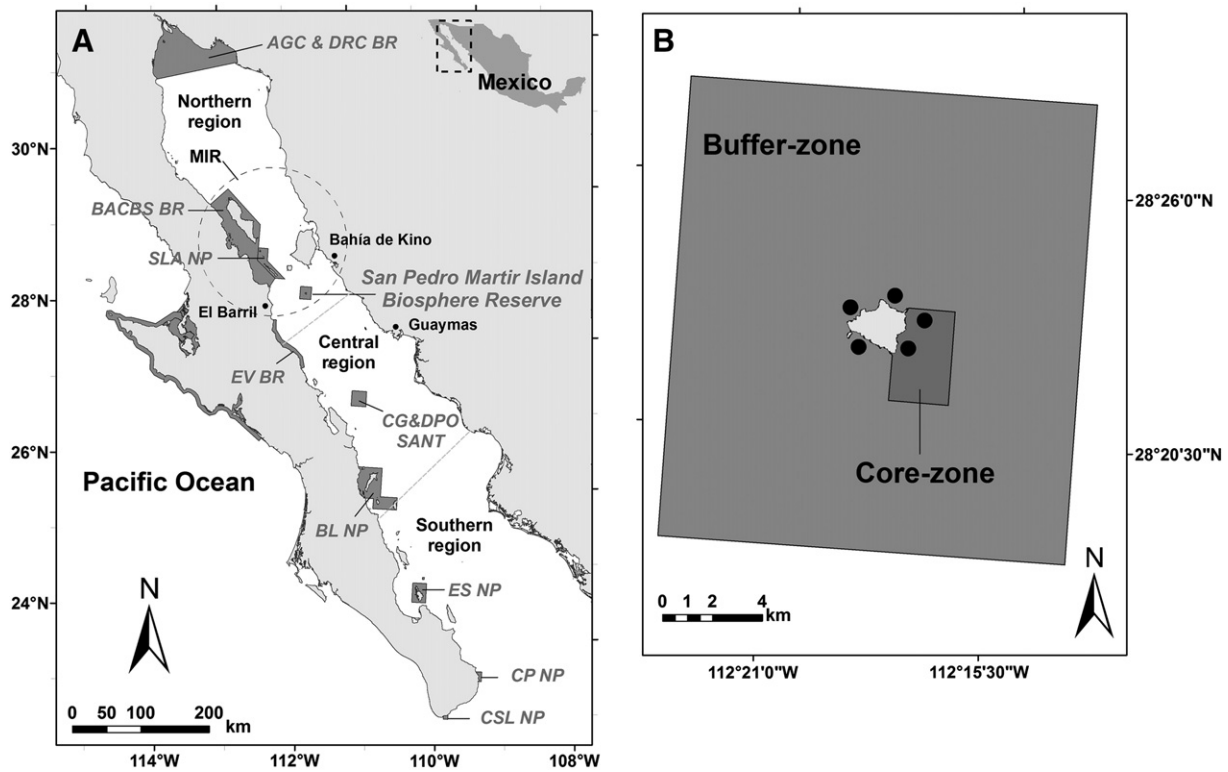


Fig. 1. Gulf of California. Panel A) Marine Protected Areas are indicated as follows: Alto Golfo de California y Delta del Rio Colorado (AGC & DRC BR), Bahía de los Ángeles, Canal de Ballenas y Salsipuedes (BACBS BR), San Lorenzo Archipelago National Park (SLA NP), El Vizcaíno (EV BR), Cuenca de Guaymas y Dorsal del Pacífico Oriental Sanctuary (CG & DPO SANT), Bahía de Loreto (BL NP), Espiritu Santo (ES NP), Cabo Pulmo (CP NP), and Cabo San Lucas (CSL NP). Midriff Islands Region (MIR). Panel B) San Pedro Mártir Island Biosphere Reserve (BR) and location of particle release sites in 3D oceanographic model.

pathways for nutrients, food and propagules (eggs, larvae, and spores), and thus connecting marine species populations (Danell-Jiménez et al., 2009; Lavín and Marinone, 2003; Sánchez-Velasco et al., 2009). The MIR contains islands of different sizes, islets, basins, sills and straits which promote a unique seascape distinguished by its species richness and biodiversity largely supported by surrounding nutrient-rich waters brought to the upper layer throughout the year by tidal mixing and convergence-induced upwelling (Alvarez Borrego, 2010; López et al., 2006, 2008).

San Pedro Mártir Island (SPMI) is the most remote island in the GC (ca. 60 km from each coast) (Murphy et al., 2002) located in the southern limit of the MIR and positioned within a transition zone between the northern and central (Lavín and Marinone, 2003). This 2.9 km-diameter island harbors large colonies of cacti (Wilder and Flegler, 2010), and its surrounding waters are rich in fish, invertebrates, sea-birds, marine mammals and sea-turtles, (CONANP-SEMARNAT, 2007). Given the unique characteristics of the island, including small size and isolation, it was decreed a Marine Protected Area (MPA) with the status of Biosphere Reserve (BR) in 2002 (DOF, 2002). In total, the reserve has an area of 302 km², including the island and two islets and 8 km² of coastal waters as core zone (no-take) and 291 km² of buffer zone where extractive activities are permitted (Fig. 1) (DOF, 2002). The island has long been used by sport fishers from continental Sonora targeting rocky reef and pelagic fishes (e.g., groupers, marlin, mahi-mahi) (Fujitani et al., 2012) and by small-scale commercial fishers from communities in both margins of the GC targeting mainly mollusk, lobsters, sea cucumbers and reef fishes (Erisman et al., 2011; Meza et al., 2008; Moreno-Báez et al., 2012). Currently, small-scale fishers within the buffer zone use three fishing gears: hookah diving, metallic traps, and hand lining. Although sport fishers are the most frequent visitors to the island, it is an important destination for small-scale commercial

fishers when fish abundances in remote fishing sites are depressed (Fujitani et al., 2012; Meza et al., 2008).

A distinctive attribute of many benthic invertebrate species (bivalves, crustaceans, echinoderms) and rocky reef fishes (snappers, groupers) is that they are structured as metapopulations: an assemblage of geographically separate subpopulations of sedentary organisms that are interconnected by the exchange of planktonic propagules (Lipcius et al., 2005). The extent to which these subpopulations are linked by the exchange of planktonic propagules is termed connectivity and can have multiple and different patterns, and implications (Lowe and Allendorf, 2010; Palumbi, 2003; Soria et al., 2012). The design of management strategies that explicitly acknowledge the complexity and dynamics of metapopulation connectivity would be most appropriate. In this sense, MPA networks, including fully protected marine reserves or no-take zones, are a tool to overcome the loss of biodiversity and the over-exploitation of fisheries that can integrate the spatial structure of marine populations in the design of management strategies (Gaines et al., 2010). The process of selecting an area or several areas to be set as MPAs is inherently a challenging assignment that involves the consideration of biophysical and human dimensions (Pollnac et al., 2010; Soria et al., 2012; Ulloa et al., 2006). As for the design of effective MPAs in general, the determination of the geographical scale, direction and magnitude of propagule dispersal, for instance through the use of oceanographic models, and its demographic and genetic impacts on distant populations is a critical area of research (Cowen and Sponaugle, 2009; Lowe and Allendorf, 2010; Soria et al., 2012). On one hand, demographic connectivity is characterized by relatively large amounts of propagules that have measurable effects in fishing activities over ecological timescales, while genetic connectivity usually involves fewer propagules that are, however, key for biodiversity conservation over evolutionary time scales,

including genetic diversity and structure that affect the evolutionary potential for adaptation (Lowe and Allendorf, 2010; Steneck et al., 2009). Since connectivity is usually assumed to decline with distance (Almany et al., 2009; Steneck et al., 2009), demographic connectivity is thought to occur only among nearby sites, while genetic connectivity could be more prevalent among distant sites. In the presence of strong directional currents, such as in the GC the importance of MPA location increases (Crowder et al., 2000; Gaines et al., 2003; Soria et al., 2012), compared to places where currents are mainly stochastic (Siegel et al., 2008).

Small, isolated MPAs as SPMI are common around the world (Mora and Sale, 2011), but are generally assumed to have low connectivity and thus low resiliency (Almany et al., 2009; Bell and Okamura, 2005). In general, small islands are deemed less important compared to big reserves because small reserves tend to be less self-sufficient and protect relatively smaller populations that produce fewer propagules (Almany et al., 2009; Claudet et al., 2008). However, contrary to this view, small islands could be completely self-sufficient for small-island endemic species (Robertson, 2001). To be self-sufficient, a MPA needs at least 10% self-recruitment (Cowen and Sponaugle, 2009). Thus, the importance of small isolated MPAs for fisheries and conservation is unclear. The peculiar location of SPMI near the limits of the northern and central GC might suggest that the island could be influenced by multiple oceanographic conditions, acting as a significant source of propagules towards different populations in the GC and thus contribute to regional fisheries and conservation.

Many benthic invertebrate species show annual reproductive cycles with intense activity throughout spring and summer, but varying in their timing, intensity and peaks, and thus entailing distinct breeding patterns (Erismann et al., 2010; Giese and Pearse, 1974). Marine currents may disperse planktonic propagules over long distances in relatively short time, but process driving patterns of connectivity might vary temporally and spatially. Changes in connectivity through the year are rarely taken into account for MPA designs, even when they have the potential to drastically change the efficacy of MPAs for meeting conservation and fishery goals. This is particularly true if spawning of marine invertebrates varies within and between species simultaneously with drastic changes in strong seasonal patterns such as winds and ocean current speed and direction (Ledezma-Vazquez et al., 2009; Marinone, 2012) that could potentially alter metapopulation connectivity over a scale of a few hundred kilometers (Amoroso et al., 2011; Becker et al., 2007; Marinone et al., 2011). As a result, patterns of connectivity can vary according to population breeding dynamics and oceanographic factors, entailing different management implications (Becker et al., 2007; Cowen and Sponaugle, 2009; Palumbi, 2003; Soria et al., 2012).

The goal of this study was to estimate connectivity patterns from SPMI as a potential source of propagules to surrounding MPAs and fishing sites. For this, we used a particle-tracking scheme based on the outputs of a three-dimensional numerical hydrodynamic model to identify the areas, including self-replenishment, to which the island could be biologically connected through the export of planktonic propagules of invertebrate and fish species. In the GC, MPAs have been established under different formats (e.g. National Parks, Marine Sanctuaries and Biosphere Reserves) mainly as an effort to reverse degradation of the environment while promoting conservation of ecosystems and biodiversity (Aburto-Oropeza et al., 2011; Bezaury-Creel, 2005). Besides MPAs, the new Fisheries Mexican Law includes no-take zones (fisheries refuges) that are intended to enhance adjacent fishing areas by density-dependent spillover and dispersal of propagules through increased abundance and biomass of organisms inside the reserve. Identifying the areas to which MPAs contribute propagules is a critical area of research, as stated in the development of the management plan of the reserve (SEMARNAT, 2011). This study provides suggestive insights supporting the role of the established MPA and its core-zone as an important but dynamic source of propagules to some fishing areas

and as a key hub in the connectivity and conservation of many sites, and discusses potential implications for the establishment of other MPAs in the GC.

2. Materials and methods

2.1. Use of local knowledge

We relied on fishers' knowledge about what, where and when they fish (Fujitani et al., 2012; Meza et al., 2008; Moreno-Báez et al., 2012) to identify the main small scale commercial benthic species fished around the island, and to delimit and select key fishing sites from which to release simulated particles. Information on fishing zones was collected through a rapid appraisal (Beebe, 1995) conducted in 2005–2006, designed to develop a preliminary, region-wide overview of the socio-economic and demographic patterns of small-scale fisheries in the northern GC. We identified 17 benthic rocky reef species, including invertebrates and fish, currently fished in the SPMI BR by the two closest fishing communities, Bahía de Kino and El Barril, showing various planktonic propagule durations centered between two weeks and one month (Table 1).

2.2. Spatial units of connectivity

To evaluate connectivity we defined spatial units of analysis by combining physical and political domains, as well as fishers' and scholars' knowledge about biophysical attributes of the region as described in detail in Soria et al. (2012). The physical domain of the study area was defined using the coast line developed by the Instituto Nacional de Estadística, Geografía e Informática, México (www.inegi.org.mx) and incorporated political boundaries, such as MPAs (CONANP, 2009) and the 100 m isobaths (Fig. 2).

2.3. Particle-tracking from a three-dimensional hydrodynamic model

We used the three-dimensional baroclinic numerical Hamburg Shelf Ocean Model (Backhaus, 1985) adapted to the GC by Marinone (2008) to estimate the velocity field of the study area. This Eulerian model has a mesh size of $\sim 1.31 \times 1.54$ km in the horizontal, and 12 layers in the vertical with the lower levels fixed at 10, 20, 30, 60, 100, 150, 200, 250, 350, 600, 1000, and 4000 m (Marinone et al., 2011). Physical forcing in the open boundary includes the main tidal components (M2, S2, N2, K2, K1, O1, P1, Ssa, and the Sa), and climatological hydrographic historical data. We also used sea surface climatological heat and fresh water fluxes. Wind forcing was based on a horizontally homogeneous seasonal climatology constructed from QuikSCAT data. The model equations are solved semi-implicitly with fully prognostic temperature and salinity fields, which allow time-dependent baroclinic motions (Marinone, 2008). Therefore the model is climatological except for the tides, with the consequence that the seasonal signal of the currents are the same every year, but the phase of the springs-neaps cycle changes from year to year. At the seasonal scale, the most important forcing mechanism is due to the Pacific, followed by the local wind (Marinone, 2003; Ripa, 1997).

We estimated particle trajectories following the advection/diffusion scheme described in Proehl et al. (2005) and Visser (2008). The Lagrangian trajectories are due to the Eulerian velocity field plus a random-walk contribution related to turbulent eddy diffusion processes. The model has advection in all directions (x, y, z, t) and adequately reproduces the main seasonal and tidal circulation for the GC (Marinone, 2008).

We released 4000 passive particles (i.e., virtual propagules) from five locations around SPMI (Fig. 1b) as proxies to represent relevant reproductive/spawning sites of commercial coastal benthic species. These sites included Punta Rabijunco (28°38'N–112°28'W) and Los Morritos (28°37'N–112°28'W) inside the core zone; and inside

Table 1

Commercial species of marine invertebrates and fish from San Pedro Mártir Island Biosphere Reserve, showing planktonic propagule duration and spawning season in the Gulf of California.

Species	Common name	Propagules duration (days)	Spawning season	References
<i>Mollusks</i>				
<i>Strombus</i> spp.	Caracol reina	12–40		Aldana-Aranda and Patino-Suarez (1998)
<i>Spondylus</i> spp.	Caracol burra	14	Jul–Aug	Soria et al. (2010)
<i>Pleuroploca</i> spp.	Caracol chile	0 ^a		Meirelles and Matthews-Cascon (2005)
<i>Hexaplex/Muricanthus</i> spp.	Chino/negro	20	Apr–Sep	Cudney-Bueno et al. (2008); Shuto (1983)
<i>Octopus</i> spp.	Pulpo	33–40	Apr–Aug	Nixon (1969); Valdez-Ornelas et al. (2008)
<i>Crustaceans</i>				
<i>Scyllarides</i> spp.	Cucaracha	240–270		Booth et al. (2005)
<i>Panulirus</i> spp.	Langosta	90–210	Mar–Sep	Vega-Velazquez et al. (1996)
<i>Echinoderm</i>				
<i>Isostichopus fuscus</i>	Pepino	28	Jul–Sep	Hearn et al. (2005); Herrero-Perezrul et al. (1999)
<i>Bony fishes</i>				
<i>Epinephelus</i> spp.	Baqueta	22–39	Jul	Macpherson and Raventos (2006); Planes et al. (1998)
<i>Mycteroperca rosacea</i>	Cabrilla sardinera	24	Mar–Jun	Aburto-Oropeza et al. (2007); Erisman et al. (2010)
<i>Mycteroperca</i> spp.	Baya, cabrilla pinta	45	Apr–May	Adamski et al. (2012); Sala et al. (2003)
<i>Paralabrax</i> spp.	Cabrilla	25–32	Mar–May	Allen and Block (2012); Erisman et al. (2010)
<i>Hoplopogrus guentheri</i>	Pargo coconaco	18–24	May–Sep	Erisman et al. (2010); Zapata and Herron (2002)
<i>Lutjanus argentiventris</i>	Pargo amarillo	22	May–Sep	Zapata and Herron (2002)
<i>Scarus</i> spp.	Pericos	30–50		Lou (1993)
<i>Caulolatilus</i> spp.	Conejo pierna	30–60	Jul–Aug	(Moser et al. (1986); Waples (1987)
<i>Scomberomorus</i> spp.	Sierra	9–18		Shoji and Tanaka (2003)

^a Intracapsular metamorphosis.

the buffer zone Arroyo Cartelón (28°386'N–112°294'W), La Cueva (28°386'N–112°313'W), and Barra Baya (28°372'N–112°313'W) in the N, NW and SW of the island, respectively. Particle trajectories were integrated for the five sites and results expressed as total export values. We conducted simulations for four release dates (May 15 and 31, and June 14 and 30 of 2007; the year was chosen arbitrarily) matching new and full moon lunar phases each month, for a total 5 sites × 4000 particles × 4 dates = 80,000 particles. Release dates were selected to match the spawning time of most benthic rocky reef species (Table 1).

We tracked particle positions (latitude, longitude, and depth) every hour after release and queried the data by means of ArcGIS 9.3 (ESRI) to obtain the number and origin of the modeled particles reaching every spatial unit of analysis. For each simulation we analyzed the data at 15, 20, and 30 days after the release, respectively, as a proxy to represent different maximum planktonic propagule durations among benthic rocky reef species (Castellanos-Martínez, 2008; Hamel et al., 2003; Herrero-Perezrul et al., 1999; Soria et al., 2010) (Table 1). We estimated the percentages of particles that settled at each coastal spatial unit relative to the total number of particles released from SPMI. Local retention was estimated as the percentages of particles that remained within the buffer zone of the SPMI over the total particles released (Botsford et al., 2009). We conducted surface drifter-tracking experiments around SPMI to investigate the near-field circulation. From May 11 to May 15, 2009, we made daily deployment of five Pacific Gyre MicroStar drifters with a Tristar drogue at 1 m depth within the core zone (Fig 1), and tracked them for 8 h. These drifters transmitted their GPS location via GlobalStar satellite telephone every 10 min (Cabrera-Ramos et al., 2010).

3. Results

3.1. Connectivity patterns

Overall, the output of the dispersion model could be characterized by four distinctive patterns, which are present, to a degree, in all simulations. First, one group of particles showed a north-east pathway dispersing along the west coast of Tiburón Island (Fig. 2A–D) and

could eventually extend to the mainland coast, reaching the main fishing grounds of Puerto Libertad, Puerto Lobos and Bahía San Jorge and eventually the Alto Golfo de California & Delta del Rio Colorado BR located ~400 km to the north from the release site. Second, another cluster of particles was dispersed south-west towards the east coast of the Baja California Peninsula, covering a wide-range including El Barril, El Vizcaíno BR, Santa Rosalía and reaching Bahía Concepción located ~200 km from the release site (Fig. 2A–D). Third, the MIR also benefited from particles exported from the Island, including San Esteban Island, San Lorenzo Archipelago NP, and Bahía de los Angeles Canal de Ballenas y Salsipuedes BR (Fig. 2A–D). The model also predicted a significant trapping of particles in the release area for each simulation, most evident for May (Fig. 2A, B).

We observed that patterns of connectivity from SPMI BR to other coastal sites were highly dynamic over the 30 days simulated, driven by changes in ocean current speed and direction (Fig. 2). These changes were consistent among propagule durations and included a steady increase in the spatial scale of connectivity from May 15th to June 30th, particularly towards northern sites (Fig. 3, for 30 days of planktonic propagule duration). Also, we observed drastic shifts along time in the coastal areas that received the largest amounts of particles (between ~ 15 and 25%) released in SPMI. For example, at 30 days, the most important site receiving particles in May 15th was an isolated island (Tortuga) located 110 km to the southwest of the release site. Although the importance of this remote island was maintained later, in May 31st the site receiving most particles was now Puerto Libertad, located ~150 km to the northeast. In June, we observed that the most important sites receiving particles from ISPM continued shifting towards the north, and on June 30th this corresponded to Bahía San Jorge located ~325 km (linear distance) to the north of the island (Fig. 3).

3.2. Mean lineal distance and frequency distributions

Particles released in mid-May showed a unimodal distance distribution where most of the particles dispersed ≤ 100 km, while in late June showed a multimodal distribution related to groups of particles going to the north and south, respectively, where most particles

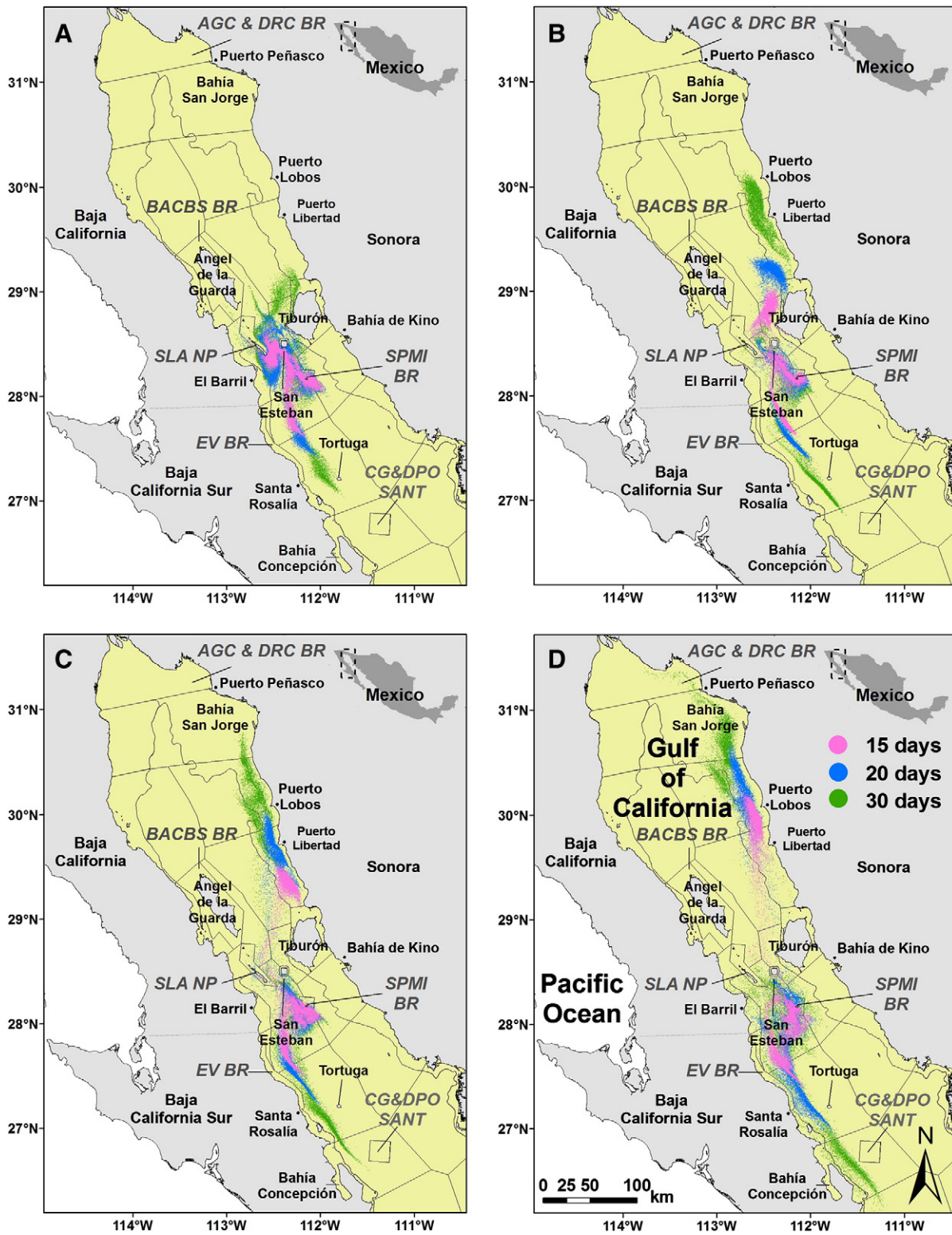


Fig. 2. Spatial units of analysis and model outputs of particles at 15, 20, and 30 days of planktonic propagule duration. Modeled propagules were released in five sites around SPMI BR and advection started in A) 15 May, B) 31 May, C) 14 June, and D) 30 June.

dispersed ≤ 300 km (Fig. 4). On average, the spatial scale of particle dispersal showed a tendency to be higher with longer planktonic propagule duration and it was about twice as large for particles going towards the north compared to the south (Figs. 2 and 4). Overall, we observed a trend where the velocity of particles (Fig. 4) and

the spatial scale of dispersal increased from May 14th to June 30th (Table 2, Fig. 4). The estimated mean linear distance of particle dispersal in May ranged between 29.7 and 103.2 km with maximum values between 87.9 and 228.3 km according to their planktonic propagule duration (Table 2) and particles concentrated within the

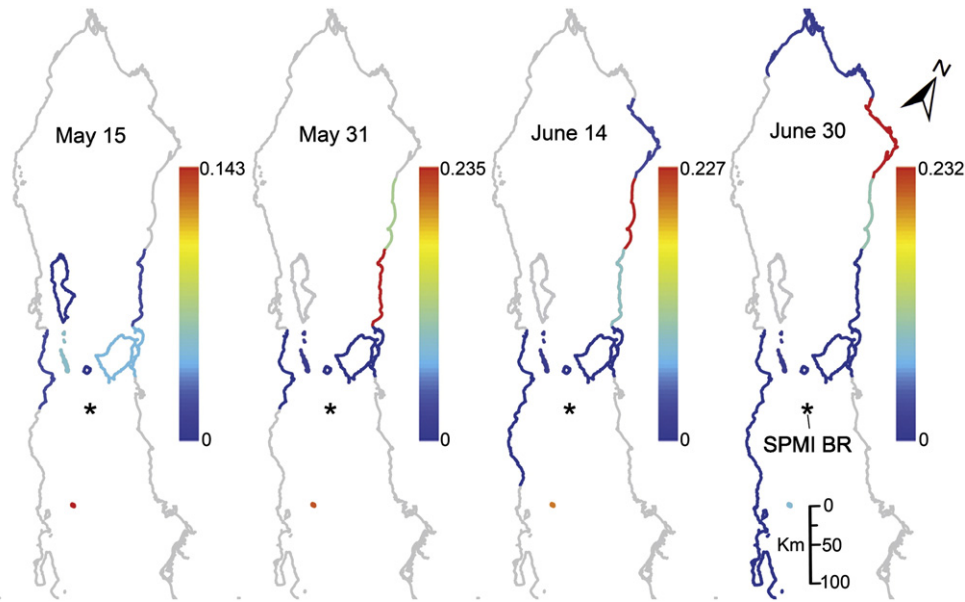


Fig. 3. Observed probabilities of propagules dispersal at each spatial unit for particles released from SPMI BR at each of four dates during May and June. Planktonic propagules duration was 30 days. Note that only coastal areas with habitat for settlement of benthic invertebrates and reef fish are included.

MIR. Particles released in June showed higher mean lineal dispersion distances according to their planktonic propagule duration (range = 64.4–162.4 km) with maximum values between 235.5 km and 393 km (Table 2, Fig. 4c & d).

3.3. Self-recruitment

On average, the proportion of particles remaining within the boundaries of SPMI (~10 km width) tended to decrease with increasing planktonic propagule duration (Fig. 5). The buffer and core zones of the reserve showed an abrupt decrease of particles within the first week [not shown]; afterwards particle percentages remained around 15% within the island area. Local trapping across planktonic propagule durations showed values $\geq 10\%$ in May to lower values in June (Fig. 5). For example, about 10% of particles remained in the boundaries of the BR after having been released on May 15th and advected for 30 days, while this value decreased to ~2.5% for particles released in June 30th (Fig. 5).

3.4. Surface drifters

The surface current pattern close to the island measured with the drifters (Fig. 6a) shows that in May 2009 the island was immersed in a fast current to the NW. The drifter data also suggest the potential for trapping (stagnation points) on the windward side of the island (SE) where currents hit it and also in the opposite leeward side (NW) (Fig. 6a). Although the drifter data cannot be used to validate the model because of the difference in space and times scales, Fig. 6b shows agreement in the far-field direction of the currents (to the NW), but the model speeds are lower, which is reasonable, considering that they are averages.

4. Discussion

4.1. Dynamics of temporal and geographical scales of connectivity

Our oceanographic model stressed that highly dynamic patterns of connectivity across short temporal but large spatial scales, could characterize a small and isolated island with MPA status. Our findings

suggest the multifaceted aspect of the benefits provided by SPMI BR for propagules export and self-recruitment. Contrary to the view that small and isolated MPAs show low connectivity, we observed high potential connectivity (*i.e.*, demographic) with a few key but distant fishing sites, and lower potential connectivity (*i.e.*, genetic) with many nearby and distant fishing sites, and with all the other four coastal neighboring MPAs, albeit not simultaneously. In addition we observed conditions for self-recruitment of the populations within SPMI BR. However, the most significant observation was that the role of the island in each of these important aspects changed dramatically over a relatively short-medium period (two months), encompassing the peak of spawning for multiple species. This highlights the dynamic nature of marine connectivity and suggests that the design of effective MPAs and MPA networks should acknowledge the spatial and temporal complexity and dynamics of patterns of connectivity and should not be designed or implemented as static entities based upon connectivity observed on a single snapshot in time or using fixed rules of the kind “one size fits all”.

The SPMI BR might have an influence on propagule dispersal involving a very large spatial scale (over 600 km along the coast). The export of particles from the island up to 400 km towards the north is on average of four times larger than previously reported results for the mainland coast of the GC (Soria et al., 2012). Although our study did not include larval behavior and thus we could be over estimating dispersal distances (Cowen and Sponaugle, 2009; Levin, 2006; Soria et al., 2012), the large influence of SPMI could be partly explained by its particular location. The island borders the northern limit of the Central GC that shows cyclonic circulation, where it bifurcates and allows some particles to disperse south toward the peninsula, while others reach the mainland shelf of the northern GC across the MIR channels. Thus, the geographic proximity to distinct oceanographic regions showing unique faunal affinities suggests relevant biological connectivity of the island. Also contributing is the timing of spawning coinciding with the reversal and intensification of currents from May to July, particularly of the northward coastal current along the mainland coast of Sonora, driven by an increase of southerly winds (Ledesma-Vazquez et al., 2009). We also confirmed that under the strong directional currents, connectivity in the GC commonly does not decrease with distance, and that the links between

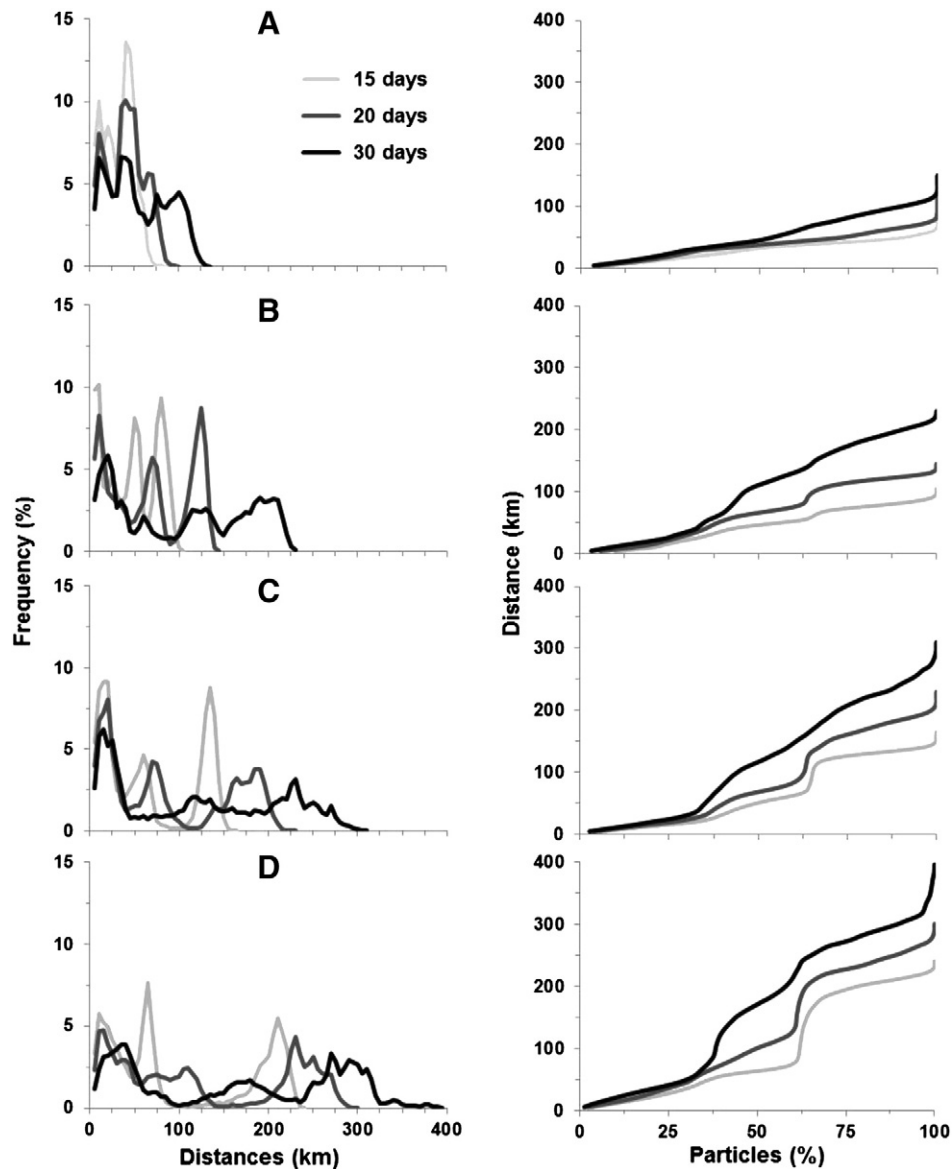


Fig. 4. Frequency distribution of particles at 15, 20 and 30 days after having been released from SPMI BR on A) 15 May, B) 31 May, C) 14 June, and D) 30 June. Panels on the right show cumulative percentages of particles as a function of distance from origin for each planktonic propagules duration and release date.

sites that may be connected *via* propagule dispersal at ecological and evolutionary time scales might be not intuitive and are highly time-sensitive.

Although our study points to the importance of a small and isolated reserve as an important source in metapopulation dynamics of some fishing sites, in MPA network resilience and in the conservation of biodiversity for multiple sites, we caution that being a hub also has the down-side of a larger likelihood of spreading risk (Watson et al., 2011). Risk could be due to natural processes (e.g., disease) or induced by anthropogenic causes (e.g., poisons used to eradicate exotic species such as rats on isolated islands) (Samaniego-Herrera et al., 2011), or possible oil-spills by cargo ships passing near the island.

Propagule exports might benefit, at different points in time, important fishing sites, such as Puerto Libertad, Puerto Lobos and Bahía San Jorge along the Sonoran Coast, and western locations along the Baja California Peninsula (El Barril, Santa Rosalía, and Bahía Concepción). Other important findings are connectivity pathways conducive to localized propagules export within the MIR. For instance, cumulative percentages of particles that have been dispersed up to 50 km (the minimum distance to reach the southern

boundaries of the San Lorenzo Archipelago BR, San Esteban and Tiburón islands) fall between 23 and 90% depending on planktonic propagule duration and release date. A higher percentage of particles

Table 2

Lineal distance (km) dispersed by particles (modeled propagules) released around SPMI BR for different 15–30 days of planktonic propagules duration.

Date		Planktonic propagule duration (days)		
		15 days	20 days	30 days
May 15	Mean	29.7	37.5	52.7
	SD	16.4	20.6	33.2
	Maximum	87.9	116.7	147.1
May 31	Mean	44.7	66.8	103.2
	SD	28.9	44.3	72.1
	Maximum	100.5	143.4	228.2
June 14	Mean	64.6	86.2	119.7
	SD	51.7	68.8	89.8
	Maximum	163.5	226.4	307.0
June 30	Mean	98.5	124.9	162.4
	SD	80.3	94.0	112.4
	Maximum	235.5	297.4	393.9

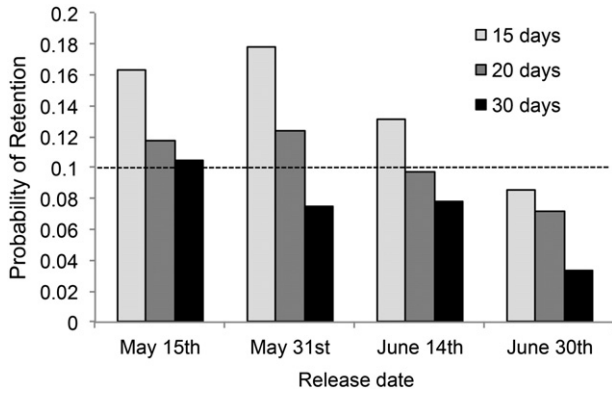


Fig. 5. Probability of local retention (y axis) of particles released at four different dates (x axis) around SPMI BR (core and buffer zones) considering three planktonic propagule durations (15, 20 and 30 days). Horizontal dashed line marks the limit needed for self-sufficiency (i.e., 10%, see text).

are expected to be dispersed less than 50 km in May in comparison with values observed throughout June, which reflects the rapid change in the range distance of connectivity patterns. Overall, the model reveals the oceanographic complexity of the study area and provides the basis for the development of ecological and evolutionary hypothesis to be tested in the field, with potential to contribute to the management and conservation of marine resources in the region.

4.2. Self-replenishment

The horizontal resolution of the numerical model does not adequately represent oceanographic processes occurring at small and medium scales (Werner et al., 2007) around the island. The size of SPMI BR is just twice the mesh size resolution of the model, indicating a much higher resolution that is needed to model local retention and highlighting the value of empirical surfer drifter data.

The circulation in the area of SPMI BR contains a quasi-permanent anticyclonic eddy (Mateos et al., 2006) and some retention can be expected in the area in general and in the island shores, especially during May. Despite the species' planktonic propagule durations (max. 30 days), the island could benefit from the retention of a fraction of propagules (less than 10%) trapped within reserve boundaries, thus contributing to self-sufficiency, which is key for a successful MPA. For instance, at least 10% of recruits should be locally produced in order to promote self-replenishment (Largier, 2003). However, according to our models the island changed from being self-sufficient in mid-May to being mainly dependent upon external sources at the end of June, albeit the drifter data suggested some retention on the windward side of the island, coincidentally near the core-zone of the reserve, which was not captured by the models. However, measurements of marine currents closer to shore are needed to assess near-field local retention in coastline bays and coves that characterize the island in more detail.

Whether self-recruitment would suffice self-replenishment demands requires further investigation in order to understand the relevance of locally produced propagules relative to distant sources that might be also contributing to local populations. The rationale underlying reserves is that they protect local populations, contributing to repopulate unprotected localities. The effectiveness of a given reserve will be influenced by the extent that local population are able to recover, either by self-recruitment or by propagules imports from distant resources (Shanks, 2009; Shanks et al., 2003). Also, for local populations inhabiting isolated reserves to persist, the size (e.g., diameter) of the reserve should be at least twice the mean dispersal distance (Botsford et al., 2003; Crowder et al., 2000; Halpern, 2003; Hastings and Botsford, 2003). The implementation of such measure would be technically difficult in the study area given its biophysical and social characteristics and the estimated geographical scale of propagule dispersal, which may vary over short-medium temporal scales. The purpose of this study was to understand the connectivity patterns of the reserve as a source of propagules, but further studies should be undertaken to test the biological connectivity of the island,

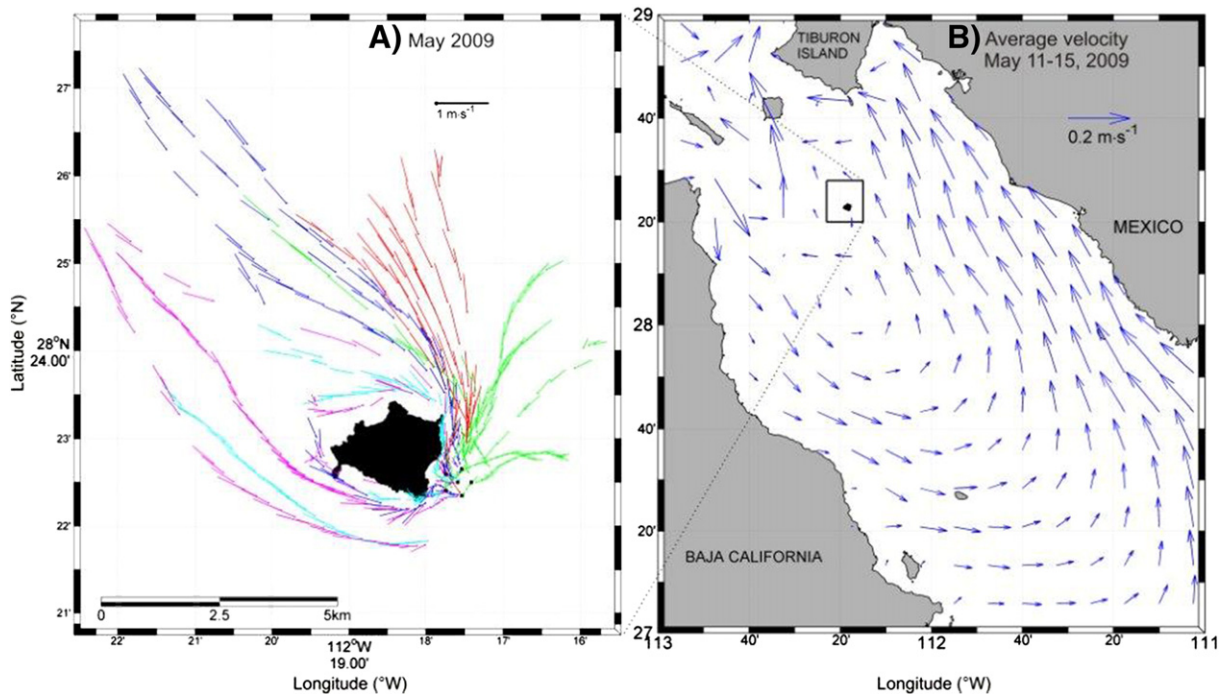


Fig. 6. Panel a) Surface currents near San Pedro Mártir Island. Each color represents a different day (May 11–15, 2009) when five GPS drifters were deployed near the black dots shown on the SE corner of the island. The drifters were tracked for around 8 h each day. Data are shown every 30 min. Panel b) May 11–15, 2009, average surface velocity vectors around SPMI from the numerical model. Only one in ten vectors is shown.

for instance with population genetics or genomic data. Future work is also needed to determine the role of self-replenishment and to incorporate biological traits and oceanographic features not addressed in this study that might affect connectivity patterns.

4.3. Potential implications for conservation and fisheries management

Effective conservation and fisheries management require understanding the spatial and temporal scales at which fishing activities and ecosystem processes take place (Fogarty and Botsford, 2007; Lipcius et al., 2005; Moreno-Báez et al., 2010). Our study shed some light on the likely geographical scale of connectivity between the SPMI BR and distant areas, suggesting an influence on multiple and diverse areas, but also on the dynamic nature of the influence radius of propagules export. This information provides support for spatial-based planning processes such as siting of MPAs, which are being internationally promoted as a useful ecosystem management tool (Douvere, 2008). For instance, the island might contribute with propagules to fishing grounds along the mainland coast and the MIR in general, and also to all existing MPAs within a certain radius and the spatial influence could vary considerably over short temporal scales. Propagule dispersal has a strong effect on population dynamics of sessile/benthic invertebrates and rocky fish species, including those whose juvenile and adult movements are negligible relative to the geographical scale of realized propagule dispersal, affecting demographic and genetic connectivity (Cowen and Sponaugle, 2009; Fogarty and Botsford, 2007; Lowe and Allendorf, 2010). We hypothesize that even though impact on fisheries stocks might be limited to a few locations, the export of propagules would at least contribute to the conservation of biodiversity, such as subpopulation viability and evolutionary adaptation.

Considering the multiple dispersal pathways associated to the island, including self-recruitment, would add more complexity and challenges to fisheries management and conservation of marine resources around the island, compared to other systems (Alberto et al., 2011; White et al., 2010). Conversely, understanding such complexity by identifying connectivity pathways might clarify where populations intersect with human activities. Marine reserves have gained special consideration because of the positive effects that they have on exploited resources, as has been recently documented for fish populations in the GC (Aburto-Oropeza et al., 2011) and elsewhere (Lester et al., 2009). In our study case, connectivity links could be protected by implementing marine reserves within comprehensive marine spatial plans and might be fixed in the location of particular habitat (e.g., rocky reef), or be adaptive network reserves that respond to dynamic ocean features and match reproductive patterns of target species and fisheries behavior. In a system such as the northern GC, marine species inhabiting the SPMI BR could act as key source of propagules and drive patterns of genetic and demographic connectivity over meso and macro scales. This could be critical for the viability and adaptation of marine species in the long-term (Pringle et al., 2011), which is one of the key aspects when implementing a MPAs.

Although outputs of modeled particles dispersal might be used as a proxy to represent potential connectivity pathways, to further improve the dispersal model we must take into consideration key biological and oceanographic (e.g., micro and meso-scales) processes (Gallego et al., 2007; Levin, 2006; Soria et al., 2012; Werner et al., 2007) that would enhance our confidence in the model. In particular, incorporating larval behavior and small-scale hydrodynamic variability near shore may render important benefits. Although we analyzed SPMI BR as a source of propagules to itself and other sites, our study did not include its role as a recipient of propagules from other sites. Our study also did not consider reproductive output or mortality, both of which are potentially important in determining patterns of connectivity (Cowen and Sponaugle, 2009). Our conclusions could be supported from polymorphic DNA markers within species (Kinlan and Gaines, 2003).

Other limitations of the model are that it does not include meso-scale nor inter-annual variability. The most important inter-annual variability in the GC is produced by the ENSO phenomenon, and it consists of an intensified influx of tropical surface water during summer (Lavin et al., 2003; Lavín and Marinone, 2003), which would carry the particles that entered the northern GC further north. There are few studies of the effect of meso-scale structures on propagule dispersal in the GC (Lavín et al., 2013; Sánchez-Velasco et al., 2013; Zamudio et al., 2008).

4.4. Conclusion

In conclusion, our study stresses the importance that a small and isolated island MPA might have when located at the boundary of distinct oceanographic systems as source of propagules for multiple regions and as potential stepping-stones. Our data indicates that this MPA is likely not self sufficient particularly for species with planktonic propagule durations larger than 15 days. Future studies should establish the origin of propagules that arrive to the island and that support fisheries for species with long planktonic propagule durations that used to be common in the island but are currently over-exploited (e.g., lobsters like *Panulirus* spp. and *Scyllarides* spp.) Moreover, patterns of connectivity might be highly dynamic covering a wide range of spatial scales (tenths to hundreds of kilometers) that could change across short temporal scales within a single reproductive season. Even though their contribution to fisheries stocks might be limited to few locations, the island would at least contribute to the conservation of biodiversity on a very large scale. The dynamic nature of marine connectivity might influence demographic and genetic connectivity and such complexity should be acknowledged when designing tools for fisheries management and conservation of marine resources like MPA networks in the region and elsewhere.

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References

- Aburto-Oropeza, O., Erisman, B., Galland, G.R., Mascareñas-Osorio, I., Sala, E., Ezcurra, E., 2011. Large recovery of fish biomass in a no-take marine reserve. *PLoS One* 6, e23601.
- Aburto-Oropeza, O., Sala, E., Paredes, G., Mendoza, A., Ballesteros, E., 2007. Predictability of reef fish recruitment in a highly variable nursery habitat. *Ecology* 88, 2220–2228.
- Adamski, K.M., Buckel, J.A., Martin, G.B., Ahrenholz, D.W., Hare, J.A., 2012. Fertilization dates, pelagic larval durations, and growth in Gag (*Mycteroperca microlepis*) from North Carolina, USA. *Bull. Mar. Sci.* 88, 971–986.
- Alberto, F., Raimondi, P.T., Reed, D.C., Watson, J.R., Siegel, D.A., Mitarai, S., Coelho, N., Serrao, E.A., 2011. Isolation by oceanographic distance explains genetic structure for *Macrocystis pyrifera* in the Santa Barbara Channel. *Mol. Ecol.* 20, 2543–2554.
- Aldana-Aranda, D., Patino-Suarez, V., 1998. Overview of diets used in larviculture of three Caribbean Conchs: Queen Conch *Strombus gigas*, Milk Conch *Strombus costatus* and Fighting Conch *Strombus pugilis*. *Aquaculture* 167, 163–178.
- Allen, L.G., Block, H.E., 2012. Planktonic larval duration, settlement, and growth rates of the young-of-the-year of two sand basses (*Paralabrax nebulifer* and *P. maculatofasciatus*: fam. Serranidae) from southern California. *Bull. South. Calif. Acad. Sci.* 111, 15–21.
- Almany, G.R., Connolly, S.R., Heath, D.D., Hogan, J.D., Jones, G.P., McCook, L.J., Mills, M., Pressey, R.L., Williamson, D.H., 2009. Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. *Coral Reefs* 28, 339–351.
- Alvarez Borrego, S., 2010. Physical, chemical, and biological oceanography of the Gulf of California. In: Brusca, R.C. (Ed.), *The Gulf of California: Biodiversity and Conservation*. University of Arizona Press, Tucson, pp. 22–48.

- Amoroso, R.O., Parma, A.M., Orensanz, J.M., Gagliardini, D.A., 2011. Zooming the microscope: medium-resolution remote sensing as a framework for the assessment of a small-scale fishery. *ICES J. Mar. Sci.* 68, 696–706.
- Argote, M.L., Amador, A., Lavín, M.F., Hunter, J.R., 1995. Tidal dissipation and stratification in the Gulf of California. *J. Geophys. Res.* 100, 16103–16118.
- Backhaus, J.O., 1985. A three-dimensional model for the simulation of the shelf sea dynamics. *Dtsch. Hydrogr. Z.* 38, 165–187.
- Becker, B.J., Levin, L.A., Fodrie, F.J., McMillan, P.A., 2007. Complex larval connectivity patterns among marine invertebrate populations. *Proc. Natl. Acad. Sci.* 27, 3267–3272.
- Beebe, J., 1995. Basic concepts and techniques of rapid appraisal. *Hum. Organ.* 54, 42–51.
- Bell, J.J., Okamura, B., 2005. Low genetic diversity in a marine nature reserve: re-evaluating diversity criteria in reserve design. *Proc. Biol. Sci.* 272, 1067–1074.
- Bezaury-Creel, J.E., 2005. Protected areas and coastal and ocean management in México. *Ocean Coast. Manage.* 48, 1016–1046.
- Booth, J.D., Webber, W.R., Sekiguchi, H., Coutures, E., 2005. Review: diverse larval recruitment strategies within the Scyllaridae. *N. Z. J. Mar. Freshw. Res.* 39, 581–592.
- Botsford, L.W., Micheli, F., Hastings, A., 2003. Principles for the design of marine reserves. *Ecol. Appl.* 13, 25–31.
- Botsford, L.W., White, J.W., Coffroth, M.A., Paris, C.B., Planes, S., Shearer, T.L., Thorrold, S.R., Jones, G.P., 2009. Connectivity and resilience of coral reef metapopulations in marine protected areas: matching empirical efforts to predictive needs. *Coral Reefs* 28, 327–337.
- Brusca, R.C., Findley, L.T., Hasting, P.A., Hendrickx, M.E., Torre, J., van der Heiden, A.M., 2005. Macrofaunal biodiversity in the Gulf of California. In: Cartron, J.L., Ceballos, G., Felger, R.S. (Eds.), *Biodiversity, Ecosystems and Conservation in Northern Mexico*. Oxford University, pp. 179–203.
- Cabrera-Ramos, C.E., Lavín, M.F., Amador, A., Ocampo-Torres, A.I., Torre, J., Rojo, M., 2010. PANGAS Lagrangian observations of surface currents in San Pedro Mártir Island (Gulf of California), with GPS-GlobalStar surface drifters. *Departamento de Oceanografía Física, CICESE, Ensenada* 43.
- Carrillo, L., Palacios-Hernández, E., 2002. Seasonal evolution of the geostrophic circulation in the northern Gulf of California. *Est. Coast. Shelf Sci.* 54, 157–173.
- Castellanos-Martínez, S., 2008. Reproducción del pulpo *Octopus bimaculatus* Verrill 1883 en Bahía de los Ángeles, Baja California, México. *Centro Interdisciplinario de Ciencias Marinas – Instituto Politécnico Nacional La Paz* 95.
- Claudet, J., Osenberg, C.W., Benedetti-Cecchi, L., Domenici, P., Garcia-Charton, J.A., Perez-Ruzafa, A., Badalamenti, F., Bayle-Sempere, J., Brito, A., Bulleri, F., Culioli, J.M., Dimech, M., Falcon, J.M., Guala, I., Milazzo, M., Sanchez-Meca, J., Somerfield, P.J., Stobart, B., Vandepere, F., Valle, C., Planes, S., 2008. Marine reserves: size and age do matter. *Ecol. Lett.* 11, 481–489.
- CONANP-SEMARNAT, 2007. Programa de Conservación y Manejo Reserva de la Biosfera Isla San Pedro Mártir. Comisión Nacional de Áreas Naturales Protegidas – Secretaría de Medio Ambiente y Recursos Naturales 218.
- CONANP, 2009. Mapa de Áreas Naturales Protegidas. Comisión Nacional de Áreas Naturales Protegidas.
- Cowen, R.K., Sponaugle, S., 2009. Larval dispersal and marine population connectivity. *Annu. Rev. Mar. Sci.* 1, 443–466.
- Crowder, L.B., Lyman, S.J., Figueira, W.F., Priddy, J., 2000. Source-sink population dynamics and the problem of siting marine reserves. *Bull. Mar. Sci.* 66, 799–820.
- Cudney-Bueno, R., Prescott, R., Hinojosa-Huerta, O., 2008. The black murex snail, *Hexaplex nigritus* (Mollusca, muricidae) in the Gulf of California, Mexico: I. Reproductive ecology and breeding aggregations. *Bull. Mar. Sci.* 83, 285–298.
- Danell-Jiménez, A., Sánchez-Velasco, L., Lavín, M.F., Marinone, S.G., 2009. Three-dimensional distribution of larval fish assemblages across a surface thermal/chlorophyll front in a semiclosed sea. *Est. Coast. Shelf Sci.* 85, 487–496.
- DOF, 2002. Decreto Área Natural Protegida con la Categoría de Reserva de la Biosfera Isla San Pedro Mártir. *Diario Oficial de la Federación. Comisión Nacional de Áreas Naturales Protegidas* 9.
- Douvere, F., 2008. The importance of marine spatial planning in advancing ecosystem-based sea use management. *Mar. Pol.* 32, 762–771.
- Erisman, B., Mascarenas, I., Paredes, G., Sadovy de Mitcheson, Y., Aburto-Oropeza, O., Hastings, P., 2010. Seasonal, annual, and long-term trends in commercial fisheries for aggregating reef fishes in the Gulf of California, Mexico. *Fish. Res.* 106, 279–288.
- Erisman, B.E., Paredes, G.A., Plomozo-Lugo, T., Cota-Nieto, J.J., Hastings, P.A., Aburto-Oropeza, O., 2011. Spatial structure of commercial marine fisheries in Northwest Mexico. *ICES J. Mar. Sci.* 68, 564–571.
- Fogarty, M.J., Botsford, L.W., 2007. Population connectivity and spatial management of marine fisheries. *Oceanography* 20, 112–123.
- Fujitani, M.L., Fenichel, E.P., Torre, J., Gerber, L.R., 2012. Implementation of a marine reserve has a rapid but short-lived effect on recreational angler use. *Ecol. Appl.* 22, 597–605.
- Gaines, S.D., Gaylord, B., Largier, J.L., 2003. Avoiding current oversights in marine reserve design. *Ecol. Appl.* 13, 532–536.
- Gaines, S.D., White, C., Carr, M.H., Palumbi, S.R., 2010. Designing marine reserve networks for both conservation and fisheries management. *Proc. Natl. Acad. Sci.* 107, 18286–18293.
- Gallego, A., North, E.W., Petitgas, P., 2007. Introduction: status and future of modelling physical-biological interactions during the early life of fishes. *Mar. Ecol. Prog. Ser.* 347, 121–126.
- Giese, A.C., Pearse, J.S., 1974. Introduction: general principles. In: Giese, A.C., Pearse, J.S. (Eds.), *Reproduction in Marine Invertebrates*. Academic Press, New York, pp. 1–49.
- Halpern, B.S., 2003. The impact of marine reserves: do reserves work and does reserves size matters? *Ecol. Appl.* 13, 117–137.
- Hamel, J.F., Ycaza-Hidalgo, R., Mercier, A., 2003. Larval development and juvenile growth of the Galapagos sea cucumber *Isostichopus fuscus*. *Inf. Bull.* 18, 3–8.
- Hastings, A., Botsford, L.W., 2003. Comparing designs of marine reserves for fisheries and for biodiversity. *Ecol. Appl.* 13, 65–70.
- Hearn, A., Martinez, P., Toral-Granda, M.V., Murillo, J.C., Polovina, J., 2005. Population dynamics of the exploited sea cucumber *Isostichopus fuscus* in the western Galapagos Islands, Ecuador. *Fish. Oceanogr.* 14, 377–385.
- Herrero-Perezrul, M.D., Reyes-Bonilla, H., García-Domínguez, F., Cintra-Buenrostro, C.E., 1999. Reproduction and growth of *Isostichopus fuscus* (Echinodermata: Holothuroidea) in the southern Gulf of California, Mexico. *Mar. Biol.* 135, 521–532.
- Kinlan, B.P., Gaines, S.D., 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* 84, 2007–2020.
- Largier, J.L., 2003. Considerations in estimating larval dispersal distances from oceanographic data. *Ecol. Appl.* 13, 71–89.
- Lavin, M.F., Palacios-Hernandez, E., Cabrera, C., 2003. Sea surface temperature anomalies in the Gulf of California. *Geofísica Inter.* 42, 363–375.
- Lavin, M.F., Castro, R., Beier, E., Godínez, V.M., 2013. Mesoscale eddies in the Gulf of California during summer: characteristics and interaction with the wind stress. *J. Geophys. Res.* 118, 1–15.
- Lavin, M.F., Marinone, S.G., 2003. An overview of the physical oceanography of the Gulf of California. In: Velasco-Fuentes, O.U., Sheinbaum, J., Ochoa, J. (Eds.), *Nonlinear Processes in Geophysical Fluid Dynamics*. Kluwer Academic Publishers, Netherlands, pp. 173–204.
- Ledesma-Vazquez, J., Johnson, M.E., Gonzalez-Yajimovich, O., Santamaria-del-Angel, E., 2009. Gulf of California geography, geological origins, oceanography, and sedimentation patterns. In: Johnson, M.E., Ledesma-Vazquez, J. (Eds.), *Atlas of Coastal Ecosystems in the Western Gulf of California*. The University of Arizona Press, Tucson, pp. 1–10.
- Lester, S.E., Halpern, B.S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B.I., Gaines, S.D., Airam, X., Warner, R.R., 2009. Biological effects within no-take marine reserves: a global synthesis. *Mar. Ecol. Prog. Ser.* 384, 33–46.
- Levin, L.A., 2006. Recent progress in understanding larval dispersal: new directions and digressions. *Integr. Comp. Biol.* 46, 282–297.
- Lipcius, R.N., Crowder, L.B., Morgan, L.E., 2005. Metapopulation structure and marine reserves. In: Norse, E., Crowder, L. (Eds.), *Marine Conservation Biology: The Science of Maintaining the Sea's Biodiversity*. Island Press, pp. 328–345.
- López, M., Candela, J., Argote, M.L., 2006. Why does the ballenas channel have the coldest SST in the Gulf of California? *Geophys. Res. Lett.* 33, L11603.
- López, M., Candela, J., García, J., 2008. Two overflows in the Northern Gulf of California. *J. Geophys. Res.* 113, C08023.
- Lou, D.C., 1993. Growth in juvenile *Scarus rivulatus* and *Ctenochaetus binotatus*: a comparison of families Scaridae and Acanthuridae. *J. Fish Biol.* 42, 15–23.
- Lowe, W.H., Allendorf, F.W., 2010. What can genetic tell us about population connectivity? *Mol. Ecol.* 19, 3038–3051.
- Macpherson, E., Raventos, N., 2006. Relationship between pelagic larval duration and geographic distribution of Mediterranean littoral fishes. *Mar. Ecol. Prog. Ser.* 327, 257–265.
- Marinone, S.G., 2003. A three-dimensional model of the mean and seasonal circulation of the Gulf of California. *J. Geophys. Res.* 108, 1–25.
- Marinone, S.G., 2008. On the three-dimensional numerical modeling of the deep circulation around Angel de la Guarda Island in the Gulf of California. *Est. Coast. Shelf Sci.* 80, 430–434.
- Marinone, S.G., 2012. Seasonal surface connectivity in the Gulf of California. *Est. Coast. Shelf Sci.* 100, 133e141 (133–141).
- Marinone, S.G., Lavín, M.F., Parés-Sierra, A., 2011. A quantitative characterization of the seasonal Lagrangian circulation of the Gulf of California from a three-dimensional numerical model. *Cont. Shelf Res.* 31, 1420–1426.
- Mateos, E., Marinone, S.G., Lavín, M.F., 2006. Role of tides and mixing in the formation of an anticyclonic gyre in San Pedro Martir Basin, Gulf of California. *Deep-Sea Res. Part II* 53, 60–76.
- Meirelles, C.A.O., Matthews-Cascon, H., 2005. Spawn and larval development of *Pleuroploca aurantiaca* (Lamarck, 1816) (Gastropoda: Fascioliidae) from northeast Brazil. *Sci. Mar.* 69, 199–204.
- Meza, A., Moreno, C., Torre, J., Rojo, M., 2008. Usos humanos en la reserva de la biosfera Isla San Pedro Mártir. *Comunidad y Biodiversidad*, Guaymas 35.
- Mora, C., Sale, P.F., 2011. Ongoing global biodiversity loss and the need to move beyond protected areas: a review of the technical and practical shortcomings of protected areas on land and sea. *Mar. Ecol. Prog. Ser.* 434, 251–266.
- Moreno-Báez, M., Cudney-Bueno, R., Orr, B.J., Shaw, W.W., Pfister, T., Torre-Cosío, J., Loaiza, R., Rojo, M., 2012. Integrating the spatial and temporal dimensions of fishing activities for management in the northern Gulf of California, Mexico. *Ocean Coast. Manage.* 55, 111–127.
- Moreno-Báez, M., Orr, B.J., Cudney-Bueno, R., Shaw, W.W., 2010. Using Fishers' local knowledge to aid management at regional scales: spatial distribution of small-scale fisheries in the northern Gulf of California, Mexico. *Bull. Mar. Sci.* 86, 339–353.
- Moser, H.G., Sumida, B.Y., Ambrose, D.A., Sandknop, E.M., Stevens, E.G., 1986. Development and distribution of larvae and pelagic juveniles of ocean whitefish, *Caulolatilus princeps*, in the CalCOFI survey region. *CalCOFI* 162–169.
- Murphy, R.W., Sanchez-Pinero, F., Polis, G.A., Aalbu, R.L., 2002. New measurements of area and distance for islands in the Sea of Cortez. In: Case, T.J., Cody, M.L., Ezcurra, E. (Eds.), *A New Island Biogeography of the Sea of Cortez*. Oxford University Press, New York, pp. 447–464.
- Nixon, M., 1969. The lifespan of *Octopus vulgaris* Lamarck. *Proc. Malacol. Soc. Lond.* 38, 529–540.

- Palacios-Hernández, E., Beier, E., Lavín, M.F., Ripa, P., 2002. The effect of winter mixing on the circulation of the northern Gulf of California. *J. Phys. Oceanogr.* 32, 705–728.
- Palumbi, S.R., 2003. Population genetics, demographic connectivity, and the design of marine reserves. *Ecol. Appl.* 13, 146–158.
- Planes, S., Parroni, M., Chauvet, C., 1998. Evidence of limited gene flow in three species of coral reef fishes in the lagoon of New Caledonia. *Mar. Biol.* 130, 361–368.
- Pollnac, R., Christie, P., Cinner, J.E., Dalton, T., Daw, T.M., Forrester, G.E., Graham, N.A.J., McClanahan, T.R., 2010. Marine reserves as linked social-ecological systems. *Proc. Natl. Acad. Sci.* <http://dx.doi.org/10.1073/pnas.0908266107>.
- Pringle, J.M., Blakeslee, A.M.H., Byers, J.E., Roman, J., 2011. Asymmetric dispersal allows an upstream region to control population structure throughout a species' range. *Proc. Natl. Acad. Sci.* 108, 15288–15293.
- Proehl, J.A., Lynch, D.R., McGillicuddy, D.J., Ledwell, J.R., 2005. Modeling turbulent dispersion on the north flank of Georges Bank using Lagrangian particle methods. *Cont. Shelf Res.* 25, 875–900.
- Ripa, P., 1997. Towards a physical explanation of the seasonal dynamics and thermodynamics of the Gulf of California. *J. Phys. Oceanogr.* 27, 597–614.
- Robertson, D.R., 2001. Population maintenance among tropical reef fishes: inferences from small-island endemics. *Proc. Natl. Acad. Sci.* 98, 5667–5670.
- Sala, E., Aburto-Oropeza, O., Paredes, G., Thompson, G., 2003. Spawning aggregations and reproductive behavior of reef fishes in the Gulf of California. *Bull. Mar. Sci.* 72, 103–121.
- Samaniego-Herrera, A., Aguirre-Muñoz, A., Rodríguez-Malagon, M., Gonzalez-Gomez, R., Torres-García, F., Mendez-Sánchez, F., Félix-Lizarraga, M., Latofski-Robles, M., 2011. Rodent eradications on Mexican islands: advances and challenges. In: Veitch, C.R., Clout, M.N., Towns, D.R. (Eds.), *Island Invasives: Eradication and Management*. IUCN, Gland, Switzerland, pp. 350–355.
- Sánchez-Velasco, L., Lavín, M.F., Peguero-Icaza, M., León-Chávez, C.A., Contreras-Catala, F., Marinone, S.G., Gutiérrez-Palacios, I.V., Godínez, V.M., 2009. Seasonal changes in larval fish assemblages in a semi-enclosed sea (Gulf of California). *Cont. Shelf Res.* 29, 1697–1710.
- Sánchez-Velasco, L., Lavín, M.F., Jiménez-Rosenberg, S.P.A., Godínez, V.M., Santamaría-del-Angel, E., Hernández-Becerril, D.U., 2013. Three-dimensional distribution of fish larvae in a cyclonic eddy in the Gulf of California during the summer. *Deep-Sea Res.* 175, 39–51.
- SEMARNAT, 2011. Programa de Manejo de la Reserva de la Biosfera Isla San Pedro Mártir. Secretaría de Medio Ambiente y Recursos Naturales 65.
- Shanks, A.L., 2009. Pelagic larval duration and dispersal distance revisited. *Biol. Bull.* 216, 373–385.
- Shanks, A.L., Grantham, B.A., Carr, M.H., 2003. Propagule dispersal distance and the size and spacing of marine reserves. *Ecol. Appl.* 13, 159–169.
- Shoji, J., Tanaka, M., 2003. Larval abundance, growth, and recruitment of Japanese Spanish mackerel *Scomberomorus niphonius* in the Seto Inland Sea, Japan. In: Browman, H.I., Skiftesvik, B. (Eds.), *26th Annual Larval Fish Conference. The Big Fish Bang*. Institute of Marine Research, Bergen, Norway, pp. 395–404.
- Shuto, T., 1983. Larval development and geographical distribution of the Indo-West Pacific murex. *Bull. Mar. Sci.* 33, 536–544.
- Siegel, D.A., Mitarai, S., Costello, C.J., Gaines, S.D., Kendall, B.E., Warner, R.R., Winters, K.B., 2008. The stochastic nature of larval connectivity among nearshore marine populations. *Proc. Natl. Acad. Sci. U. S. A.* 105, 8974–8979.
- Soria, G., Munguía-Vega, A., Marinone, G., Moreno-Báez, M., Martínez-Tovar, I., Cudney-Bueno, R., 2012. Linking bio-oceanography and population genetics to assess larval connectivity. *Mar. Ecol. Prog. Ser.* 463, 159–175.
- Soria, G., Tordecillas-Guillen, J., Cudney-Bueno, R., Shaw, W., 2010. Spawning induction, fecundity estimation, and larval culture of *Spondylus calcifer* (Carpenter, 1857) (Bivalvia: Spondylidae). *J. Shellfish. Res.* 29, 143–149.
- Steneck, R.S., Paris, C.B., Arnold, S.N., Ablan-Lagman, M.C., Alcalá, A.C., Butler, M.J., McCook, L.J., Russ, G.R., Sale, P.F., 2009. Thinking and managing outside the box: coalescing connectivity networks to build region-wide resilience in coral reef ecosystems. *Coral Reefs* 28, 367–378.
- Ulloa, R., Torre, J., Bourillón, L., Gondor, A., Alcantar, N., 2006. Planeación ecorregional para la conservación marina: Golfo de California y costa occidental de Baja California Sur. Informe Final a The Nature Conservancy. Comunidad y Biodiversidad, A.C., Guaymas, México 153.
- Valdez-Ornelas, V., Aburto-Oropeza, O., Torreblanca-Ramírez, E., Danemann, D.G., 2008. Bahía de los Ángeles: recursos naturales y comunidad. In: Danemann, D.G., Ezcurra, E. (Eds.), *Recursos pesqueros*. SEMARNAT, Mexico, pp. 429–456.
- Vega-Velazquez, A., Espinoza-Castro, G., Gomez-Rojo, C., 1996. Pesquería de la langosta *Panulirus* spp. In: Casas-Valdez, M., Ponce-Díaz, G. (Eds.), *Estudio del potencial pesquero y acuicola de Baja California Sur*. Centro de Investigaciones Biológicas del Noroeste, La Paz, pp. 227–261.
- Visser, A.W., 2008. Lagrangian modelling of plankton motion: from deceptively simple random walks to Fokker-Planck and back again. *J. Mar. Sys.* 70, 287–299.
- Walker, B.W., 1960. The distribution and affinities of the marine fish fauna of the Gulf of California. *Syst. Zool.* 9, 123–133.
- Waples, R.S., 1987. A multispecies approach to the analysis of gene flow in marine shore fishes. *Evolution* 41, 385–400.
- Watson, J.R., Siegel, D.A., Kendall, B.E., Mitarai, S., Rassweiler, A., Gaines, S.D., 2011. Identifying critical regions in small-world marine metapopulations. *Proc. Natl. Acad. Sci.* 108, E907–E913.
- Werner, F.E., Cowen, R.K., Pars, C.B., 2007. Coupled biological and physical models: present capabilities and necessary developments for future studies of population connectivity. *Oceanography* 20, 54–69.
- White, C., Selkoe, K.A., Watson, J.R., 2010. Ocean currents help explain population genetic structure. *Proc. R. Soc. B.* 277, 1685–1694.
- Wilder, B.T., Fleger, R.S., 2010. Dwarf giants, guano, and isolation: vegetation and floristic diversity of San Pedro Mártir Island, Gulf of California, Mexico. *Proc. San Diego Soc. Nat. Hist.* 42, 1–24.
- Zamudio, L., Hogan, P., Metzger, E.J., 2008. Summer generation of the southern Gulf of California eddy train. *J. Geophys. Res.* 113, C06020.
- Zapata, F.A., Herron, P.A., 2002. Pelagic larval duration and geographic distribution of tropical eastern Pacific snappers (Pisces: Lutjanidae). *Mar. Ecol. Prog. Ser.* 230, 295–300.